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FACIAL MIMICRY AND PLAY: A COMPARATIVE STUDY IN CHIMPANZEES AND GORILLAS

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ABSTRACT

Play fighting, a common form of mammalian play, can escalate into aggression if playful motivation is misinterpreted and not shared by players. In primates, playful facial expressions and mimicry can be performed to signal and share playful motivation. Here we compare play facial expressions (Play Face, PF: lower teeth exposed; and Full Play Face, FPF: upper and lower teeth exposed) and their mimicry in captive chimpanzees and lowland gorillas, during play fighting. These two species have different social dynamics, with social cohesion being lower - and play possibly riskier - in gorillas than in chimpanzees. Thus, we hypothesized that gorillas would perform redundant play faces more often to avoid misunderstanding (prediction 1). However, the two species are phylogenetically very close and possess a similar biology. Thus, we hypothesized that both species could perform Rapid Facial Mimicry (RFM: response within 1 second) and Delayed Facial Mimicry (DFM: response occurring between 1 to 5 seconds), which may have different roles in play modulation (prediction 2). Gorillas performed more FPF than chimpanzees and FPFs lasted longer than the less intense PF (prediction 1 supported). RFM was present in both species, whereas DFM was present only in chimpanzees (prediction 2 not fully supported). DFM may be performed by chimpanzees to modulate the session at a later stage of the interaction and favor inter-individual cohesion. RFM prolonged play sessions and may be performed to communicate playful motivation to the playmate thus demonstrating that animals integrate contextual information into their understanding of others' states and intentions.

Key words: *Pan troglodytes*, *Gorilla gorilla gorilla*, emotional mimicry, play, social cohesion

INTRODUCTION

Among all social activities, play behavior is notable for its versatility, plasticity, and unpredictability (Palagi, Burghardt, Smuts, Cordoni, Dall'Olio et al., 2016; Špinka, Newberry, & Bekoff, 2001). In humans, play is important during childhood for improving cognitive, physical, emotional and social skills (Ginsburg, 2007). In other mammals, social play can provide individuals with short term benefits (e.g. physical training: Martin & Caro, 1985; anxiety reduction: Norscia & Palagi, 2011; access to social groups: Antonacci, Norscia, & Palagi, 2010) and long term benefits (e.g. increase of the chance of survival: Fagen & Fagen, 2004; training for the unexpected: Špinka et al., 2001).

Play fighting (also known as rough-and-tumble play or play wrestling) is a highly variable and common form of contact play that can be observed in a broad range of species, including human and non-human primates (Pellis & Pellis, 2017). Whatever the species considered, play fighting bears the risk of escalation into serious fighting (Fagen, 1981). When one playmate uses disproportionate force or fails to comply with the rules that ensure reciprocity (turn-taking), the play session becomes unbalanced and may lead to overt aggression (Fagen, 1981; Palagi et al., 2016; Pellegrini, 2009; Pellis & Pellis, 1998, 2016; Pellis, Pellis, & Reinhart, 2010).

Specific facial expressions, vocalizations, movements, gestures, and postures are performed during play fighting to signal the non-seriousness of the context to reduce the risk of escalation to aggression and prolong play sessions (Bekoff, 1995; Cordoni & Palagi, 2011, 2013; Mancini, Ferrari, & Palagi, 2013a; Palagi & Cordoni, 2012; Palagi et al., 2016; Waller & Dunbar, 2005). While some of these play signals are “borrowed” from serious functional contexts (such as agonistic, anti-predatory and mating behavior; Bekoff & Byers, 1981; Fagen, 1993; Pellis, 1988; Pellis & Pellis, 2009), some others are unique to play (e.g. head rotation, Petrů, Špinka, Charvátová, & Lhota, 2009).

In humans, facial expressions can be performed in a context dependent way and provide information on core affect, social messages, incipient actions, situations, or appraisals (Nelson &

Russell, 2013). Also in non-human primates facial expressions can be used to communicate in a contextually dependent way (e.g. silent bared teeth display in macaques; Beisner & McCowan, 2014). However, spontaneous facial expressions - as opposed to fake, deceptive or exploitative expressions (Godfray & Johnstone, 2000; Calvo, Gutiérrez-García, Avero, & Lundqvist, 2013) - can also inform the observers about the mood of the performer because they are considered as honest signals (e.g. anger: Reed, DeScioli, & Pinker, 2014; sadness: Reed & DeScioli, 2017; crying: Schmidt & Cohn, 2001; enjoyment: Calvo et al., 2013). Consistently, among other functions facial expression in humans can inform the observer of the expresser's emotion, and positive emotions such as happiness, more than negative emotions, are largely recognized from facial expressions across cultures and languages (Nelson & Russell, 2013). In both human and nonhuman animals, spontaneous facial expressions can unveil the internal states of individuals (Gallese, 2003; Gallese, Keysers, & Rizzolatti, 2004; de Waal & Preston, 2017).

The relaxed open-mouth display, or play face, is a unique trademark of play behavior that has been observed in many species of nonhuman primates (lemurs: Palagi, Norscia, & Spada, 2014; Norscia & Palagi, 2016; macaques, Scopa & Palagi, 2016; Preuschoft, 1992; Preuschoft & van Hooff, 1995,1997; geladas, Palagi & Mancini, 2011; great apes, Cordoni & Palagi, 2013; Palagi, 2006, 2008; Palagi & Cordoni, 2012; Palagi, Antonacci & Cordoni, 2007; Waller & Cherry, 2012) and other animals (American black bear: Henry & Herrero, 1974; South American sea lions: Llamazares-Martín, Scopa, Guillén-Salazar, & Palagi, 2017).

In humans, laughter (visual component) and smile are facial expressions that are performed to communicate a positive affective state, including during play (Panksepp, 2004). Both laughter and smile can take different forms. For example, humans can produce voiced, songlike laughs and other laugh variants that include unvoiced grunts, pants, and snortlike sounds, which are less likely to elicit positive responses than voiced smiles (Bachorowski & Owren, 2001). From the morphological point of view, three main types of smiles have been classically described: i) the play smile, in which jaw drops and the lip corners raise; ii) the Duchenne smile, in which the lip corners

and the cheeks raise and the skin around the eyes crinkle with an involvement of the *orbicularis oculi* and *zygomaticus major*; iii) the duplay smile, including a lip corner raise, a jaw drop, and a cheek raise (Fogel, Nelson-Goens, & Hsu, 2000). A further categorization includes reward smiles (symmetrical and accompanied by eyebrow raising), affiliative smiles (involving lip pressing) and dominance smiles (asymmetrical and accompanied by nose wrinkling and upper-lip raising; Rychlowska, Jack, Garrod, Schyns, Martin, & Niedenthal, 2017). A recent study found that people associate Duchenne smiles with psychological proximity (e.g. familiarity) and non-Duchenne smiles with psychological distance (Bogodistov & Dost, 2017). Children can perform different types of smiles depending on the type of play (e.g. physical, with objects, etc.) and on the playmate (e.g. father, mother) (Dickson, Walker, & Fogel, 1997; Sarra & Otta, 2001).

To communicate their playful mood and avoid misunderstanding, great apes generate two variants of the relaxed open-mouth display: Play Face (PF), in which only the lower teeth are exposed and Full Play Face (FPF), in which both upper and lower teeth are exposed (Palagi, 2008; van Hooff & Preuschoft, 2003). It has been posited that these two displays may be the ritualized versions of the biting movement that precedes the play bite, particularly frequent during play fighting (Andrew, 1963; Palagi, 2006, 2008). It has also been proposed that in gorillas and chimpanzees the FPF may be derived from a combination of the PF and the bared-teeth display (a signal of appeasement, submission and/or affiliation) as it contains morphological elements of both expressions (Preuschoft & van Hooff, 1995; Waller & Cherry, 2012). Overall, extant theory supports the idea that PF and FPF are gradation of the same expression, with FPF being a more intense version of PF.

No consensus has been reached so far on the role of facial displays in expressing emotional states, because animals cannot report on their own emotional experience and the link between specific facial expressions and emotions has not yet been fully clarified (Bliss-Moreau & Moadab, 2017). Nonetheless, a variety of studies indicates that homologies exist. For example, the brain areas that are used for face processing are similar in human and nonhuman primates (e.g. macaques:

Tsao, Moeller, & Freiwald, 2008), and there are marked morphological similarities between the nonhuman primate bared-teeth display and the human smile, as well as between the nonhuman primate play face and the human face associated with laughter (Parr & Waller, 2006; Parr, Waller, & Fugate, 2005; Preuschoft, 1992; Preuschoft & van Hooff, 1995, 1997). Similar to the nonhuman primate play face, human laughter (an expression that is innate and not learned by imitation; Black, 1984) may also have originally emerged in association with the motivation to play. In children, laughter is more commonly associated with free play than with verbal exchanges, such as during jesting (Panksepp, 2004).

In both human and nonhuman animals, playful facial signals can be replicated by the partner, a phenomenon referred to as "facial mimicry" (Iacoboni, 2009). In its broadest and most neutral sense, mimicry is the replication of an observed posture, movement or facial expression that does not imply true imitation (Sonnby-Borgström, 2016). True imitation requires the recognition of the goal of the demonstrator and the achievement of the goal by copying the same sequence of action (Call & Tomasello, 1995; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). Different from the replication of non-emotional behavioral patterns (behavioral mimicry), the replication of facial expressions can be relevant to emotional sharing because it involves emotional mimicry (i.e., the replication of emotional displays; Hess & Fischer, 2014). In both human and nonhuman primates, mimicry can be either rapid or delayed and these two forms of mimicry seem to have, at least partly, different origins and functions (Iacoboni, 2009; Dimberg, Thunberg, & Grunedal, 2002).

Rapid Facial Mimicry (RFM) is the response that occurs within a second after the perception of the stimulus (Iacoboni, 2009), a pattern that is consistent with the definition of emotional mimicry (Dimberg & Thunberg, 1998; Hess & Fischer, 2014). This response may involve the mirror neuron system as well as other neural circuits (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Ferrari, Gallese, Rizzolatti, & Fogassi, 2003; Gallese, Fadiga, Fogassi, Rizzolatti, 1996; Likowski et al., 2012). This system was discovered in the premotor and parietal cortices of

monkeys, with its motor neurons firing both when the monkey performs an action and when it observes a similar action performed by another individual (Ferrari et al., 2003). An equivalent system also exists in humans and may allow the perception of others' emotions (Iacoboni & Dapretto, 2006), even though humans may also simulate emotional experience to recognize it (Barsalau, 2008). Mimicry is a crucial component of play in children (Karpatschof, 2013). Moreover, it has been clearly demonstrated that RFM in both nonhuman primates (e.g. Davila-Ross, Menzler, & Zimmermann, 2008; Mancini et al., 2013a; Scopa & Palagi, 2016) and dogs (Palagi, Nicotra, & Cordoni, 2015) increases the duration of play sessions.

Delayed Facial Mimicry (DFM) usually occurs with a delay of one to five seconds after the perception of the stimulus (Dimberg & Thunberg, 1998; Dimberg et al., 2002). In humans with neurodevelopmental pathologies a delayed response (more than 1s) is associated with neurological anomalies (e.g. white matter hyperplasia and reduced long-range axons in Autism Spectrum Disorder subjects, Oberman, Winkielman, & Ramachandran, 2009; degeneration of basal ganglia network and associated motor areas in Parkinson Disease subjects; Livingstone, Vezer, McGarry, Lang & Russo, 2016). In non-pathological subjects, a response is delayed when indirect neural pathways are involved, as more synapses are traversed (Ferrari, Bonini & Fogassi, 2009). The delayed response (even when considering the acoustic component of laughter only) may allow the replication of the playful mood at a later stage of interaction (Davila-Ross, Allcock, Thomas, & Bard, 2011; Mancini et al., 2013a; Schmidt & Cohn, 2001).

Both RFM and DFM are likely to have important roles, albeit with a different timing, in the regulation of playful encounters. In the present study we compare the playful facial expressions (PF and FPF) and the role of RFM and DFM in the play fighting of two close human relatives, chimpanzees (*Pan troglodytes*) and lowland gorillas (*Gorilla gorilla gorilla*). Gorillas separated from the human/chimpanzee lineage 10 million years ago, and humans and chimpanzees diverged around 6 million years ago (Scally et al., 2012). The close phylogenetic relationship among the three genera (*Gorilla*, *Pan* and *Homo*) may be particularly relevant to understand the biological

basis of the mimicry in facial communication during social play. *Pan troglodyte*s and *Gorilla gorilla gorilla* share some features, such as highly developed cognitive abilities and a prolonged immature phase, with weaning not being complete until 5-6 years of age (Goodall, 1986; Stanton, Lonsdorf, Pusey, Goodall, & Murray, 2014; Watts & Pusey, 1993). Similarly, humans are characterized by a long period of immaturity (Bjorklund, 1997). These long periods of immaturity are important because in all these species the frequency of play fighting is highest during infancy and the juvenile period (Cordoni & Palagi, 2011; Palagi et al., 2007; Waller & Cherry, 2012; Pellegrini, 2009). Additionally, in many large-brained mammals (including great apes and humans) play fighting, as a form of social play, is an important tool to acquire information about others (Paquette, 1994; Pellegrini, Dupuis, & Smith, 2007; Pellis et al., 2010).

Despite these similarities, the two study species show marked differences in their social structure and levels of inter-individual bonding (Cordoni, Norscia, Bobbio, & Palagi, 2018). Western lowland gorillas (*Gorilla gorilla gorilla*) live in breeding groups that usually comprise one adult male (silverback), several adult females and immature offspring (Harcourt & Stewart, 2007; Yamagiwa, Kahekwa & Basabose, 2003). Adult females commonly aggregate around the silverback (Parnell, 2002). The spatial proximity to the silverback results in a close spatial association among the adult females who are not closely related to one another, and do not have reciprocal social bonds. When the silverback dies, the group breaks up and the females join other groups. As a result, gorillas are characterized by low affiliative contacts and inter-individual cohesion (Cordoni et al., 2018; Harcourt & Stewart, 2007; Stokes, Parnell, & Olejniczak, 2003; Yamagiwa et al., 2003). In contrast, chimpanzees live in multimale-multifemale groups (fission-fusion society) in which both males and females can engage in enduring social relations (Goodall, 1986; Gruber & Clay, 2016). Males form strong social bonds because they tend to stay in their natal group (male philopatry) and their level of kinship is high; females can establish long-term relationships, e.g. via grooming exchange and agonistic support (Goodall, 1986; Gruber & Clay, 2016). The limited available evidence suggests that the differences in inter-individual affiliation and social cohesion between

these two species may have an influence on the performance of play signals (Flack, Jeannotte, & de Waal, 2004; Waller & Cherry, 2012). Based on the similarities and differences between *Pan troglodyte*s and *Gorilla gorilla gorilla* we put forth several hypotheses on the display of playful facial signals and the role of mimicry, empirically grouped into two main predictions.

Prediction 1: Lowland gorillas display playful facial signals more frequently and with greater exaggeration than chimpanzees

In communication systems, signal redundancy (prolonged and more intense signals) can be modulated to increase the probability that the message is correctly conveyed (Hebets et al., 2016). Playful facial signals can serve multiple functions during play fighting (with some differences between monkeys and apes: Palagi et al., 2016; Pellis, Pellis, Reinhart, & Thierry, 2011). Their redundancy can be increased by human and nonhuman mammals in potentially risky situations to avoid misunderstanding between players (Bekoff, 1995; Henry & Herrero, 1974; Palagi et al., 2016; Power, 2000). Infants and pre-school children can show more salient play smiles and laughter (e.g., more exaggerated, broader, longer in duration) during contact play, including play fighting (Fogel, Hsu, Shapiro, Nelson-Goens, & Secrist, 2006; Justin, 1932; Sarra & Otta, 2001). Great apes, including wild chimpanzees, captive bonobos and Western lowland gorillas, can preferentially show FPF, the most intense form of play face, during rough and potentially risky play sessions (Palagi, 2006, 2008; van Lawick-Goodall, 1968; Waller & Cherry, 2012). Given the different levels of inter-individual affiliation in chimpanzees and lowland gorillas we hypothesize that gorillas should show more redundant facial signaling because play occurring between weakly bonded individuals is riskier. If so, we predict that compared to chimpanzees, gorillas would show playful facial signals more frequently in its most redundant version, the FPF.

Predition 2: Both rapid and delayed facial mimicry are present and relevant to the playful interactions in chimpanzees and gorillas

As a form of emotional mimicry, RFM is one of the modalities through which two or more interacting individuals can share their playful mood (Palagi & Scopa, 2017). Consistent with this hypothesis, several studies, on a variety of primate species, have shown that RFM increases the synchronization of playful actions by partners and the duration of playful interactions (Davila-Ross et al., 2011; Mancini et al., 2013a; Scopa & Palagi, 2016). In chimpanzees, the co-occurrence of audible laughing by partners was closely linked to the maintenance of playful contact (Davila-Ross et al., 2011). A similar function has been hypothesized for laughter (visual and acoustic component) in both children and adult humans (Weisfeld, 1993). Given these consistent findings on primates, we hypothesize that mimicry of play signals is likely to be important for all the great apes, including gorillas. If so, we predict that RFM should be present during play in both chimpanzees and lowland gorillas (prediction 2a). Specifically, we hypothesize that it is the occurrence of RFM - and not just the mere presence of non-mimicked play faces - that is most effective in prolonging the play sessions (prediction 2b). Both chimpanzees and lowland gorillas possess a prolonged immature phase during which play fighting is expressed at high rates (Cordoni et al., 2018; Herrmann, Wobber, & Call, 2008; MacDonald, 1994; Palagi et al., 2007). Hence, as occurs with laughter in chimpanzees (Davila-Ross et al., 2011) and humans (Gervais & Wilson, 2005; Mehu et al., 2007), we predicted that both gorillas and chimpanzees would modulate their facial mimicry responses during play and show not only RFM but also DFM (prediction 2c).

METHODS

Ethics Statement

Because the study was purely observational the committee of the University of Pisa (Animal Care and Use Board) waived the need for a permit. The study was conducted with no manipulation of animals.

Subjects and Data Collection

The study groups

The study was carried out on one colony of 15 chimpanzees (*Pan troglodytes*) and two colonies of lowland gorillas (*Gorilla gorilla gorilla*) - a family and a bachelor group for a total of 16 individuals - housed at the ZooParc de Beauval (St. Aignain sur Cher, France). The composition of the study colonies is presented in Table 1. We did not find any significant difference in the age of the subjects of the two species (Mann-Whitney test $U = 94.00$, $N_G = 17$, $N_C = 15$, $p = 0.206$).

The three groups occupied similar enclosures composed by an indoor and outdoor facility of about 200 m^2 and 2000 m^2, respectively. The enclosures were comparable in terms of hiding (e.g., vegetation, rocks, holes) and resting places (hammocks and platforms). The indoor facilities were equipped with trunks, lianas, ropes, and platforms so that animals could move freely. All the three outdoor enclosures were delimited by an artificial moat. The management schedule of the three groups was the same. Animals received food (vegetables, seeds and grains, branches with green leaves) four times per day approximately at the same hours and twice a week the three groups received environmental enrichments such as sticks, rags, and small plastic tanks. Water was available *ad libitum*. No stereotypic or aberrant behaviors were observed in the groups.

Data collection

We collected data from October to December 2015. The observations took place daily over a 6-h period that spanned morning and afternoon (including feeding times), both in indoor and outdoor facilities. Before commencing systematic data collection, the observers (authors and one assistant) underwent 35 hrs of training to become skilled in identifying each individual and the various patterns of play to be scored. The same observers collected data on both species. To recognize play patterns, including play fighting, an animal was simultaneously followed by all observers and the data were later compared and discussed. Training ended when the observations produced a Cohen's kappa >0.85 (Kaufman & Rosenthal, 2009). To avoid the possibility that different forms of play (e.g., gentle vs. rough forms) could bias the comparisons, only play fighting (or rough-and-tumble play), the form of play critical for this study, was considered for subsequent analyses. In Table 2 the motor patterns composing play fighting are listed and defined.

The observers collected data daily on both chimpanzees and gorillas according to the following schedule: Day A - gorillas in the morning, chimpanzees in the afternoon; Day B - gorillas in the afternoon, chimpanzees in the morning.

Data on non-play behavior were collected using scan sampling and provided a broader social context to evaluate the data on play fighting, such as agonistic encounters, grooming and contact sitting (Altman, 1974). The behavior patterns were scored as absent or present every 5 min for all animals in the group. This yielded 59.5 hr of observation for chimpanzees, 65.0 hr for the gorilla family and 41.0 hr for the bachelor group. To obtain detailed data on play fighting an all occurrences sampling method was used, so that all instances of play fighting occurring during the period of observation were recorded (Altman, 1974). Since play interactions in the great apes are highly predictable, the observer could easily anticipate the forthcoming bout. This permitted observers to turn on the camera well before the beginning of the playful interaction. Moreover, when play bouts were prolonged and/or involved many subjects, the camera worked in continuum to avoid losing the interactions. This yielded 738 play fights for chimpanzees and 647 for gorillas. For the all occurrence sampling, one or both observers (depending on the number of play sessions concurrently occurring) videotaped the play fights. The videotaped sequences were then analysed and coded using the programs Kinovea 0.8.15 and VLC 2.2.1. Before commencing systematic analysis of the videotaped sequences, the observers tested their inter-observer reliability in behavioral coding, until reaching a Cohen's κ value > 0.85 (Kaufman & Rosenthal, 2009). During the video-analysis, this procedure was repeated every 3 hours of video, with both observers scoring the same 15 min of video, to ensure consistent inter-observer reliability for each behavioral item scored. Cohen's κ value was never less than 0.85.

A play session began when one partner invited another individual to play, or directed any playful pattern toward it. If the partner ignored the invitation this was not considered as a play session. A session ended when playmates ceased their activities, that is, one of them moved away or

a third individual interrupted the previous interaction. If another play session began after 10 s, that session was counted as new.

As for the definition of polyadic sessions, we used the following criteria. If the individuals A and B were playing and C joined in, the session shifted from dyadic to polyadic and the two sessions were considered as distinct. Similarly, if one of the three animals dropped out, the session shifted into a dyadic session and it was considered as a new session. When at least one of the players changed during a polyadic/dyadic playful interaction, that session was considered as a new session. We calculated the duration of each play session at the dyadic level. In case of polyadic play, we calculated the duration of the session involving each dyad as follows a-b-c = a-b; a-c; b-c.

For each bout of play fighting we recorded i) the identities of the players (i.e., name, sex, age), ii) the behavioral patterns performed and facial expressions emitted as they occurred in chronological order (Table 2), iii) the number of players involved and iv) the duration of the play bout (Play Duration) in seconds. For each facial expression performed (PF and FPF) we determined the exact duration in seconds via frame-by-frame video analysis. The duration was calculated from the first frame showing the separation of the inferior from the superior lip until the first frame showing the two lips closed again.

Data analysis for prediction testing

Prediction 1: Facial play signals in the two species

To evaluate if the two variants of the playful facial expression (i.e., Play Face - PF - versus Full Play Face - FPF) were performed with different rates by the two species, an index defined as [FPF-PF]/[FPF+PF], was used. In this way, the relative measure of the total number of play faces performed by each subject was obtained. This index provides a single measure suitable for comparisons across groups and between individuals because it is independent from differences in the absolute rates of emission of these signals that vary markedly across individuals and species.

Owing to the non-normal data distribution (Kolmogorov-Smirnov, $p<0.05$), we applied the nonparametric Mann-Whitney U for two independent samples (Mundry & Fischer, 1998; Siegel &

Castellan, 1988) to test for differences in the play face index between species and determine whether gorillas performed one of the two facial play signals (FPF/PF) significantly more than chimpanzees or not. Only the subjects showing at least two facial expressions were included in the analysis to make sure that the individuals had the opportunity to perform both PF and FPF (the number of subjects is reported for each statistical test in the Results). The nonparametric Exact Wilcoxon Signed-rank test for paired samples (Mundry & Fischer, 1998; Siegel & Castellan, 1988) was used to check for the difference in the duration of PF and FPF within species, at the individual level.

Prediction 2: Presence of facial mimicry in the two species and variables affecting play duration

To test for the presence of facial mimicry we analyzed the playful facial expression (PF or FPF) emitted by the receiving animal (the observer) after it observed a facial expression by a partner (the trigger). Thus, the trigger was the first animal emitting the playful facial expression and the observer was the second. Due to the non-normal distribution of data (Kolmogorov-Smirnov, ns), we applied the nonparametric Exact Wilcoxon Signed-rank test (Mundry & Fischer, 1998; Siegel & Castellan, 1988) to compare the frequency of PF+FPF performed in direct visual contact with the trigger with the frequency of PF+FPF performed when the stimulus emitted by the trigger was not visible to the receiver (control condition). Only the subjects who perceived at least 1 stimulus were included in the analysis. The analyses were carried out on different datasets so no correction of the level of significance was necessary.

In the analysis, we distinguished between Rapid Facial Mimicry (RFM), when the observer mirrored the facial expression of the trigger within 1 sec from the perception of the stimulus and Delayed Facial Mimicry (DFM), when the observer mirrored the facial expression between 1-5 seconds from the perception of the stimulus (Davila-Ross et al., 2008; Mancini et al., 2013a; Palagi et al., 2015). To reliably assess if the response performed by the observer was really elicited by the stimulus emitted by the trigger, we took into account only those interactions in which the observer

looked at the trigger and did not show any kind of playful facial expression in the 1 sec prior to the emission of the stimulus by the trigger. We evaluated the attentive state of the observer by considering its head orientation (Demuru, Ferrari & Palagi, 2015; Scopa & Palagi, 2016). When the trigger was in front of the observer (i.e., within the range of its stereoscopic view, direct visual contact), we considered the facial expression as perceived. When the observer was facing away from the trigger (without direct visual contact), we considered the facial expression as not perceived. All the doubtful cases due to lateral views were discarded from the analyses (Figure 1). Facial mimicry latencies were measured frame-by-frame with 4 csec accuracy starting when the observer perceived the stimulus by the trigger and ending when the observer began to perform the response (the first lip opening detectable by the experimenter).

To verify if the occurrence of RFM and/or other variables affected Play Duration, defined as the mean duration of play sessions by each dyad involved, we distinguished between three clusters of play interactions: 1) play sessions punctuated by at least one occurrence of RFM, 2) play sessions characterized by the occurrence of at least one signal seen by the player but not followed by RFM and, 3) play sessions in which the player did not receive any signal, either because the signal was not released or because the signal was released but was unperceivable (Figure 1). To assess which factors may affect Play Duration in the two species we ran a General Linear Mixed Model. This analysis allows the presence of repeated measures and the inclusion of both fixed factors (the variables of interest, whose values come from the study sample and are exhaustive) and random factors (not coming from on-purpose sampling but from a random sample that can be used as a control variable). Owing to its flexibility, GLMM is particularly suitable to analyze heterogeneous data derived from naturalistic, non-experimental settings in a rigorous manner.

Play Duration was the dependent variable and followed a normal distribution after log-transformation (Anderson-Darling, ns) (Table 3). The fixed factors considered were: individual characteristics (sex, age and rank of the players, expressed as Normalized David's Scores - NDS, see de Vries, Stevens, & Vervaecke, 2006; Flack et al., 2004), relationship quality (measured by the

frequencies of grooming and contact sitting), play interaction clusters (see above for definition), number of players (dyadic play *vs* polyadic play) (Table 3). For chimpanzees, player identities (each player was included in the analysis) were entered in the GLMM as *random factors* (Table 3). For gorillas, the random factors were both player identities (each player was included in the analysis) and group membership (family *vs* bachelor) (Table 3). We tested models for each combination of variables of interest, spanning from the null model to the model including all the fixed factors (full model). To select the best model, we used the Akaike's Corrected Information Criterion (AICc), a measure for comparing mixed models based on the −2 (Restricted) log likelihood. The model with a lower value of AICc was considered to be the best model. To measure the extent of improvement of the best model compared to the next best models, we calculated the difference ($\Delta AICc_i$) between the AICc value of the best model and the AICc value for each of the other models. We considered as competing the models showing a $\Delta AICc < 6$ (Symonds & Moussalli, 2011). To assess the relative strength of each candidate model, we employed $\Delta AICc_i$ to calculate the Akaike weight (w_i). The w_i (ranging from 0 to 1) is the weight of evidence or probability that a given model is the best model, taking into account the data and set of candidate models (Symonds & Moussalli, 2011).

To calculate the effect size for the independent data we used the Cohen's d, as this is the most appropriate effect size measure if two groups have similar standard deviations and are of similar size. Analyses were performed with SPSS 20.0 (SPSS Inc., Chicago, IL, USA). All the analyses were two-tailed and the level of significance was set at 5%.

RESULTS

Prediction 1: Play facial displays in the two species

Gorillas performed more FPF (number of FPF per sec of play: mean 0.021 ±0.003 SE) than PF (mean 0.009 ±0.003 SE) compared to chimpanzees (FPF: mean 0.013 ±0.003 SE; PF: mean 0.006 ±0.002 SE) as the play face index was higher in gorillas (Exact Mann-Whitney U = 4.5; $N_{chimpanzees}=13$; $N_{gorillas}=12$; p=0.0001; Cohen's d = 2.54, Figure 2). In gorillas, FPF was significantly

longer than PF (Exact Wilcoxon Signed-Rank test, T=3.00; ties=0; $N_{gorillas}$= 9; p=0.02) (Figure 3), whereas there was no significant difference in chimpanzees (Exact Wilcoxon Signed-Rank test, T=22.50; ties=0; $N_{chimpanzees}$=10; p=0.643). Patterns of FPF in gorillas and PF in chimpanzees are shown in Supplementary Videos.

Prediction 2: Presence of facial mimicry in the two species and variables affecting play duration

In summary, the analyses showed that RFM was present during play fighting in both species, whereas DFM was present only in chimpanzees. RFM in gorillas and in chimpanzees is shown in Supplementary Videos.

Chimpanzees - The frequency of PF+FPF performed in direct visual contact with the trigger (stimulus perceived) was significantly higher compared to when the stimulus emitted by the trigger was not visually perceived by the receiver (no visual contact) (Figure 1). This was the case for both RFM (response < 1 sec; Exact Wilcoxon Signed-Rank test, T=0.00; ties=1; $N_{chimpanzees}$ = 8; p=0.016) and DFM (response between 1 and 5 secs; Exact Wilcoxon Signed-Rank test, T=0.00; ties=2; $N_{chimpanzees}$ = 8; p=0.031) (Figure 4a). During chimpanzee RFM, the level of mirrored responses (PF→PF; FPF→FPF) did not differ from that of non-mirrored responses (PF→FPF; FPF→PF) (Exact Wilcoxon Signed-Rank test, T=4.00; ties=6; N = 13; p=0.125) (Figure 5).

Gorillas - The frequency of PF+FPF performed in direct visual contact with the trigger (stimulus perceived) was significantly higher compared to when the stimulus emitted by the trigger was not visually perceived by the receiver (no direct visual contact). This finding was significant for RFM (Exact Wilcoxon Signed-Rank test, T=0.00; ties=0; $N_{gorillas}$ = 8; p=0.008), but not for DFM (Exact Wilcoxon Signed-Rank test, T=16.00; ties=0; $N_{gorillas}$ = 8; p=0.813) (Figure 4b). During gorilla RFM, the frequency of mirrored responses (PF→PF; FPF→FPF) was significantly higher

compared to that of non-mirrored responses (PF→FPF; FPF→PF) (Exact Wilcoxon Signed-Rank test, T=0.00; ties=3; N = 12; p=0.004) (Figure 5).

GLMM analyses revealed the following best models explaining the variance of Play Duration.

Chimpanzees - There were three competing models. The first one included the fixed variables "RFM, Polyadic/dyadic, delta Normalized David's Scores" (AICc=905.853) and explained about 68.38% of the variance. The second (AICc = 908.384; explaining 19.29% of the variance) and the third model (AICc = 909.390; explaining 11.67% of the variance) included the variables "RFM, Polyadic/dyadic" and "RFM X Polyadic/dyadic", respectively (Table 4; 5). In all the three competing models, RFM (Figure 6a) and the number of players (mean duration of dyadic sessions = 40.96 ±1.97SE; mean duration of polyadic sessions = 27.02 ±2.16SE) remained significant (Table 4).

Gorillas - There were four competing models. The first one included the fixed variables "RFM, Polyadic/dyadic" (AICc = 921.634) and explained about 45.29% of the variance. The second (AICc = 922.732; explaining 26.16% of the variance), the third (AICc = 923.288; explaining 19.81% of the variance) and the fourth model (AICc = 924.922; explaining 8.75% of the variance) included the variables "RFM, Polyadic/dyadic, Grooming", "RFM, Polyadic/dyadic, Grooming, delta Normalized David's Scores", "RFM, Polyadic/dyadic, delta Normalized David's Scores", respectively (Table 4;5). In all the four competing models, the only variables that always remained significant were RFM (Figure 6b) and the number of players (mean duration of dyadic sessions = 26.90 ±1.47SE; mean duration of polyadic sessions = 13.28 ±2.22SE) (Table 4).

DISCUSSION

Consistent with studies on other groups of chimpanzees and lowland gorillas (Cordoni & Palagi, 2011; Waller & Cherry, 2012), the present findings show that both Play Face (PF) and the more intense Full Play Face (FPF) are performed during play fighting. However, our results show

that compared to chimpanzees, lowland gorillas preferentially performed the most intense form of the signal (favoring FPF over PF), and for a longer mean duration than PF (increased signal redundancy; Prediction 1 confirmed).

We found that the frequency of PF/FPF performed by a subject after perceiving the play face of the playmate was significantly higher compared to when the play face of the playmate was not perceived. This result suggests that the play face performed after seeing the play face of the playmate can be due to mimicry rather than to the spontaneous generation of the facial expression. Both chimpanzees and gorillas performed Rapid Facial Mimicry (RFM) during play fighting (Prediction 2a supported). RFM, but not the mere production of playful facial displays, was associated with longer sessions of play fighting in both species (Prediction 2b supported). Also, for both species, the number of players (i.e., dyadic versus polyadic play) influenced the duration of play fighting. Another species difference that did emerge from the study was that only chimpanzees showed Delayed Facial Mimicry (DFM; prediction 2c not fully supported).

Play fighting can be riskier in lowland gorillas than chimpanzees because gorillas are not as socially bonded as chimpanzees (Cordoni et al., 2018; Goodall, 1986; Gruber & Clay, 2016; Harcourt & Stewart, 2007; Stokes et al., 2003; Yamagiwa et al., 2003). These species differences in social organization may account for the differences in the performance of play signals during play fighting. In lowland gorillas the greater frequency of the most intense version of the play face (FPF) and the longer duration of these facial displays, may represent a strategic tool to avoid misunderstanding and ensure the maintenance of playful interactions (Bekoff, 1995; Bekoff & Allen, 1998; Pellis & Pellis, 1996). Consistent with this possibility, Palagi and colleagues (2007) found that juvenile lowland gorillas increased the frequency of play faces (PF+FPF) in particularly risky situations, such as when the opportunity to move away from the partner was reduced (i.e., indoor enclosure) or when play fighting occurred between males. As they become adults, the males of this species switch from play to serious (and sometimes fierce) fighting to gain dominance (Breuer, Robbins, Boesch, & Robbins, 2012). Waller & Cherry (2012) found that Western lowland

gorillas performed the FPF more frequently during rough and potentially risky play sessions. In chimpanzees, we found no preferential display of FPF over PF, which is in line with a previous study that revealed no difference in the levels of FPF and PF according to the type of play in this species (Palagi, 2006). It is possible that in chimpanzees the risk remains low even when play becomes rougher and/or other modulation mechanisms are present (Cordoni et al., 2018). However, a greater occurrence of FPF has been reported to be associated with rough play in wild chimpanzees (van Lawick-Goodall, 1968) and in captive bonobos (*Pan paniscus)* (Palagi, 2006, 2008). These divergent findings suggest that further investigation is necessary to disentangle the relationship between the display of play signals and the play context in the *Pan* genus. A previous investigation on geladas (*Theropithecus gelada*) showed that also in monkeys, and not only in apes, FPF can be used in a contextually dependent way (Palagi & Mancini, 2011). The study found that FPF was performed by adult more than immature geladas and that FPF was preferentially displayed towards younger partners. FPF in geladas includes the bared-teeth component, which in this species is an appeasement/affiliative signal. This signal of affiliation incorporated in the play face might help individuals to maintain the playful motivation especially during those interactions engaged by subjects who differ in their body size, age and status. Being more clearly perceivable than the PF, the FPF may be performed to reassure the other player of the low risk of the interaction. In humans, context and partner identity can influence which of the various positive facial expressions are displayed. Rychlowska et al. (2015) found that three functionally distinct subtypes of smiles (i.e., pleasure smiles, affiliative smiles and dominance smiles) vary according to the different history of people, thus explaining cross-cultural variation in emotional expression and smile behavior. In 6-12 month-old children, the duration and amplitude of play smiles is context dependent and higher during contact play with the mother than with other individuals (Fogel et al., 2006). In pre-school children, exaggerated laughter, laughter and open-mouth smiles (as compared to closed-mouth smiles) are most often associated with mock aggression, which is a risky form of play (Justin, 1932; Sarra & Otta, 2001). Hence, the risk of the playful interaction seems to modulate the performance

of different facial emotional expressions in both humans and other primates. In order for play to produce its benefits, not only must animals communicate their playful mood and engage in playful interactions, but they must also avoid disrupting play (Pellis & Pellis, 2009).

RFM and DFM (reported for the first time in this study in chimpanzees) might modulate the play session with a different timing. RFM immediately communicates to the playmate that the playful intention has been perceived, accurately interpreted, and most probably shared. DFM might be performed by chimpanzees to replicate the playful intention also at a later stage of the interaction, to prolong the positive social interaction and favor social cohesion. Another explanation for the presence of a delayed response in chimpanzees (DFM) may be a possible audience effect on response elicitation, with this effect prevailing in chimpanzees owing to their higher social cohesion compared to gorillas (Cordoni et al., 2018). Kaminski, Hynds, Morris, & Waller, (2017) found that dogs produced significantly more facial expressions when observed by human demonstrators than when they were not attended. In this respect, dog facial expressions may not just be emotional displays *per se*, but can have communicative functions.

The presence and similar effect of rapid facial mimicry (RFM) on play duration in both chimpanzees and gorillas suggest that RFM may be related to the dynamics of play fighting more than to the social cohesion of group mates. As a matter of fact, RFM and not the mere emission of the playful facial signals prolonged the playful interactions in both species. This is in line with previous studies on other primates (acoustic laughter: chimpanzees, Davila-Ross et al., 2011; RFM: geladas, Mancini et al., 2013a,b) and non-primate species (RMF, domestic dogs, Palagi et al., 2015). In humans, several studies have demonstrated that the occurrence of emotional mimicry is related to the motivation that individuals have to carry out the interaction and not just to the relationship existing between them (Hess & Fisher, 2013, 2014; Parkinson, 2011). Emotional disclosure is not simply due to the amount of time two individuals spend together, but rather to the expression and sharing of emotions (Fisher & Manstead, 2008). Emotions are preferentially expressed to a receiver that is expected to respond appropriately, thus moving from simple emotion

expression to emotional sharing (Clark, Fitness, & Brissette, 2004). In human groups, emotional sharing (group-based emotion, Fischer & Manstead, 2008) strengthens the bonds between conspecifics and helps determine social dynamics because emotions are differentially distributed across group members (Keltner & Haidt, 1999). Hatfield, Cacioppo & Rapson (1992) suggested that the function of mimicry is to synchronize and coordinate the interaction between subjects and, thereby, to facilitate mutual involvement. The play face, by unveiling unambiguous positive emotions, may elicit the same positive emotional state in the observer, informed by the presence of RFM (Decety & Meyer, 2008; Mehu et al., 2007).

Through RFM, emotions can be propagated because, by rapidly and automatically replicating the same expression, an observer can experience the same emotional state underpinning the facial expression of the trigger (Hatfield, Cacioppo, & Rapson, 1994; Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Gallese et al., 2004; Palagi et al., 2015). This mechanism is known as *same face-same emotion* process and differs from the controversial facial feedback hypothesis (supported by Strack, Martin, & Stepper, 1988; but recently refuted by Wagenmakers et al., 2016). The *facial feedback* hypothesis stipulates that people's affective state can be influenced by their own facial expressions, even when they are cognitively induced and are not the result of an emotional experience (Strack et al., 1988; Wagenmakers et al., 2016). Hence, the *same face-same emotion* hypothesis and the *facial feedback* hypothesis differ for the involvement of the emotional experience in the facial replication process. Contextual factors can bias the emotional mimicry response when it does occur (Wieser & Brosch, 2012) and emotional replication is unlikely to be the only mechanism by which emotions, especially negative ones, are propagated (Dezecache, Jacob, & Grezes, 2015). For example, the expression of certain negative emotions may elicit a matching response (e.g. as it occurs in cry contagion; Jordan & Thomas, 2017) whereas some others may not (e.g. anger may elicit fear; Dezecache et al., 2015). However, RFM is likely critical for the propagation of a positive playful mood (Norscia & Palagi, 2016; Palagi & Scopa, 2017). In nonhuman primates, the capacity to quickly mirror the same facial expression of the first performer

may be adaptive as it allows an individual to share the playful mood of the interacting partner and fine-tune its own motor sequences accordingly (Palagi, 2008; Palagi & Mancini, 2011). These abilities are important prerequisites to promote social affiliation and manage a playful interaction successfully (Palagi et al., 2016; Pellis & Pellis, 2009). Facial mimicry may convey important information to the triggering performer by signaling not only that the stimulus of "non-serious intent" has been perceived but also that it has been accurately interpreted. This facial exchange reduces the potential ambiguity coming from the lack of response or incongruent response.

Our results show that as well as the presence of RFM, the number of players also significantly affected the duration of play fighting sessions (Table 4). In particular, the play sessions with more than two players (polyadic) had a shorter duration than the sessions with only two players (dyadic) in both species. The more the players involved, the more difficult for any one player to engage in emotional sharing and synchronize movements with all the other playmates. Hence, the risk of escalation into serious fighting increases.

In conclusion, in chimpanzees and lowland gorillas the extent to which animals communicate their positive, playful mood via the production of facial displays seems to be related to the social cohesion of the players, which can make play more or less risky in these species (Cordoni et al., 2018). Mimicking facial displays, on the other hand, seems to be associated with the maintenance of play fighting, by possibly enhancing emotional sharing and the synchronization of actions. Overall, chimpanzees and gorillas are able to generate the play face in a context (both phylogentic and momentary) appropriate manner, demonstrating that they integrate contextual information into their understanding of others' states and intentions.

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REFERENCES

Altmann, J. (1974). Observational study of behaviour sampling methods. *Behaviour, 49*, 227-265.

Andrew, R. J. (1963). The origin and evolution of the calls and facial expressions of the primates. *Behaviour, 20*(1), 1-107

Antonacci, D., Norscia, I., & Palagi, E. (2010). Stranger to familiar: wild strepsirhines manage xenophobia by playing. *Plos one, 5*(10), e13218.

Bachorowski, J. A., & Owren, M. J. (2001). Not all laughs are alike: voiced but not unvoiced laughter readily elicits positive affect. *Psychological Science*, 12: 252-257.

Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psycholo*gy, *59*, 617-645.

Beisner, B. A., & Mccowan, B. (2014). Signaling context modulates social function of silent bared-teeth displays in rhesus macaques (*Macaca mulatta*). *American Journal of Primatology, 76*(2), 111–121.

Bekoff, M. (1995). Play signals as punctuation: the structure of social play in canids. *Behavior, 132*, 419-429. doi:10.1163/156853995X00649

Bekoff, M., & Allen, C. (1998). Intentional communication and social play: how and why animals negotiate and agree to play. In M. Bekoff & J. A. Byers (Eds.), *Animal Play: Evolutionary, Comparative, and Ecological Perspectives* (pp. 97-114). Cambridge: Cambridge University Press.

Bekoff, M., & Byers, J. A. (1981). A critical reanalysis of the ontogeny of mammalian social and locomotor play: an ethological hornet's nest. In K. Immelmann, G. Barlow, L.

Petrinovich & M. Main (Eds.), *Behavioral development: The Bielefeld interdisciplinary conference* (pp. 296-337). New York: Cambridge University Press.

Black, D. W. (1984). Laughter. *Journal of the American Medical Association, 252*(21), 2995-2998.

Bliss-Moreau, E., & Moadab, G. (2017). The Faces Monkeys Make. In J.M. Fernández-Dols & J.A. Russel (Eds.), *The Science of Facial Expression* (pp. 153-171). Oxford (UK): Oxford University Press.

Bogodistov, J., & Dost, F. (2017). Proximity begins with a smile, but which one?: associating non-Duchenne smiles with higher psychological distance. *Frontiers in Psychology, 8*, 1374. doi: 10.3389/fpsyg.2017.01374

Breuer, T., Robbins, A. M., Boesch, C., & Robbins, M. M. (2012). Phenotypic correlates of male reproductive success in western gorillas. *Journal of Human Evolution, 62*(4), 466-472.

Bjorklund, D. F. (1997). The role of immaturity in human development. *Psychological Bulletin*, *122*(2), 153-169.

Call, J., & Tomasello, M. (1995). Use of social information in the problem solving of orangutans (*Pongo pygmaeus*) and human children (*Homo sapiens*). *Journal of Comparative Psychology*, *109,* 308–320. doi:10.1037/0735-7036.109.3.308

Calvo, M. G., Gutiérrez-García, A., Avero, P., & Lundqvist, D. (2013). Attentional mechanisms in judging genuine and fake smiles: Eye-movement patterns. Emotion, 13(4), 792.

Carr L., Iacoboni M., Dubeau, M. C. Mazziotta, J. C., & Lenzi, G. L. (2003). Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 5497-5502. doi:10.1073/pnas.0935845100

Clark, M. S., Fitness, J., & Brissette, I. (2004). Understanding people's perceptions of relationships is crucial to understanding their emotional lives. In M. B. Brewer & M. Hewstone (Eds.), *Emotion and motivation* (pp. 21-47). Malden, MA: Blackwell.

Cordoni, G., & Palagi, E. (2011). Ontogenetic trajectories of chimpanzee social play: similarities with humans. *PlosONE, 6(11)*, e27344. doi:10.1371/journal.pone.0027344

Cordoni, G., & Palagi, E. (2013). Smiling and primate play faces: origins and functions. *Human Evolution*, *28*, 79-89.

Cordoni, G., Norscia, I., Bobbio, M., & Palagi. E. (2018). Differences in play can illuminate differences in affiliation: A comparative study on chimpanzees and gorillas. *PLoS ONE* 13(3), e0193096. https://doi.org/10.1371/journal.pone.0193096.

Davila-Ross, M., Allcock, B., Thomas, C., & Bard, K. A. (2011). Aping expressions? Chimpanzees produce distinct laugh types when responding to laughter of others. *Emotion*, *11(5)*, 1013-1020. doi:10.1037/a0022594

Davila-Ross, M., Menzler, S., & Zimmermann, E. (2008). Rapid facial mimicry in orangutan play. *Biology Letters*, *4*, 27-30. doi: 10.1098/rsbl.2007.0535

de Vries, H., Stevens, J. M. G., & Vervaecke, H. (2006). Measuring and testing the steepness of dominance hierarchies. *Animal Behaviour*, *71(3)*, 585-592. doi:10.1016/j.anbehav.2005.05.015

de Waal, F. B. M., & Preston, S. D. (2017). Mammalian empathy: behavioural manifestations and neural basis. *Nature Reviews Neuroscience*, 18(8), 498.

Decety, J., & Meyer, M. (2008). From emotion resonance to empathic understanding: a social developmental neuroscience account. *Development and Psychopathology*, *20*, 1053-1080. doi:10.1017/S0954579408000503

Demuru, E., Ferrari, P.F., & Palagi, E. (2015). Emotionality and intentionality in bonobo playful communication. Animal Cognition, 18(1), 333-344. doi: 10.1007/s10071-014-0804-6

Dezecache, G., Jacob, P., & Grezes, J. (2015). Emotional contagion: its scope and limits. *Trends in Cognitive Sciences*, *19*, 297-299. doi: 10.1016/j.tics.2015.03.011

Dickson, K. L., Walker, H., & Fogel, A. (1997). The relationship between smile type and play type during parent-infant play. *Developmental Psychology, 33*(6), 925.

di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: a neurophysiological study. *Experimental Brain Research, 91*, 176-180. doi:10.1007/BF00230027

Dimberg, U., & Thunberg, M. (1998). Rapid facial reactions to emotional facial expressions. *Scandinavian Journal of Psychology, 39*, 39–45.

Dimberg, U., Thunberg, M., & Grunedal, S. (2002). Facial reactions to emotional stimuli: automatically controlled emotional responses. *Cognition and Emotion*, *16*, 449-471. doi: 10.1080/02699930143000356

Fagen, R. (1981). *Animal Play Behavior*. New York: Oxford University Press.

Fagen, R. (1993). Primate juvenile and primate play. In M. E. Pereira & L. A. Fairbanks (Eds.), *Juvenile Primates* (pp. 182-196). Oxford: Oxford University Press.

Fagen, R., & Fagen, J. (2004). Juvenile survival and benefits of play behaviour in brown bears, *Ursus arctos*. *Evolutionary Ecology Research, 6*(1), 89-102.

Ferrari, P. F., Bonini, L., & Fogassi, L. (2009). From monkey mirror neurons to primate behaviours: possible "direct" and "indirect" pathways. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1528), 2311–2323. http://doi.org/10.1098/rstb.2009.0062

Ferrari, P. F., Gallese, V., Rizzolatti, G., & Fogassi, L. (2003). Mirror neurons responding to the observation of ingestive and comunicative mouth actions in monkey ventral premotor cortex. *European Journal of Neuroscience, 17*, 703-714.

Fischer, A. H., & Manstead, A. S. R. (2008). Social functions of emotions. In M. Lewis, J. M. Haviland-Jones, & L. Feldman Barrett (Eds.), Handbook of emotions (pp. 456-470). New York: The Guilford Press.

Flack, J. C., Jeannotte, L. A., & de Waal, F. B. M. (2004). Play signaling and the perception of social rules by juvenile chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 118(2),* 149-159. doi: 10.1037/0735-7036.118.2.149

Fogel, A., Hsu, H. C., Shapiro, A. F., Nelson-Goens, G. C., & Secrist, C. (2006). Effects of normal and perturbed social play on the duration and amplitude of different types of infant smiles. *Developmental Psychology, 42*(3), 459.

Fogel, A., Nelson-Goens, G. C., & Hsu, H. C. (2000). Do different infant smiles reflect different positive emotions?. *Social Development, 9*(4), 497-520.

Gallese, V. (2003). The manifold nature of interpersonal relations: the quest for a common mechanism. *Philosophical* Transactions *of the* Royal Society, *358*, 517-528. doi:10.1098/rstb.2002.1234

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain, 119*, 593-609. doi:10.1093/brain/119.2.593

Gallese, V., Keysers, C., & Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in Cognitive Sciences, 8*, 396-403. doi:10.1016/j.tics.2004.07.002

Gervais, M., & Wilson, D.S. (2005). The evolution and function of laughter and humor: a synthetic approach. *Quarterly Review of Biology, 80*, 395–430.

Ginsburg, K. R. (2007). The importance of play in promoting healthy child development and maintaining strong parent-child bonds. *Pediatrics, 119*(1), 182-191.

Godfray, H. C. J., & Johnstone, R. A. (2000). Begging and bleating: the evolution of parent–offspring signalling. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 355(1403), 1581-1591.

Goodall, J. (1986). *The chimpanzees of Gombe: patterns of behavior*. Boston (MA): Harvard University Press.

Gruber, T., & Clay, Z. (2016). A comparison between bonobos and chimpanzees: a review and update. *Evolutionary Anthropology, 25*, 239-252. doi: 10.1002/evan.21501.

Hatfield, E., Cacioppo, J. T., & Rapson, R. L. (1992). Primitive emotional contagion. In M. S. Clark (Ed.), *Review of personality and social psychology: Vol. 14. Emotion and social behavior* (pp. 151-177). Thousand Oaks, CA: Sage.

Hatfield, E., Cacioppo, J. T., & Rapson, R. L. (1994). *Emotional Contagion*. Cambridge (UK): Cambridge University Press.

Harcourt, A. H, & Stewart, K. J. (2007). Gorilla society: what we know and don't know. *Evolutionary Anthropology, 16,* 147-158. doi: 10.1002/evan.20142.

Hebets, E. A., Barron, A. B., Balakrishnan, C. N., Hauber, M. E., Mason, P. H., & Hoke, K. L. (2016). A systems approach to animal communication. *Proceedings of the Royal Society B: Biological Sciences, 283*(1826), 20152889. http://doi.org/10.1098/rspb.2015.2889

Henry, J. D., & Herrero, S. M. (1974). Social play in the American black bear: its similarity to canid social play and an examination of its identifying characteristics. American Zoologist, 14(1), 371-389.

Herrmann, E., Wobber ,V., & Call, J. (2008). Great apes' (*Pan troglodytes, Pan paniscus, Gorilla gorilla, Pongo pygmaeus*) understanding of tool functional properties after limited experience. *Journal of Comparative Psychology, 122,* 220-230. doi:10.1037/0735-7036.122.2.220.

Hess, U., & Fischer, A. (2013). Emotional mimicry as social regulation. *Personality and Social Psychology Review, 17,*142-157. doi:10.1177/1088868312472607

Hess, U., & Fischer, A. (2014). Emotional mimicry: why and when we mimic emotions. *Social and Personality Psychology Compass, 8,* 45-57. doi:10.1111/spc3.12083

Iacoboni, M. (2009). Imitation, empathy, and mirror neurons. *Annual Review of Psychology, 60,* 653-670. doi:10.1146/annurev.psych.60.110707.163604

Iacoboni, M., & Dapretto, M. (2006). The mirror neuron system and the consequences of its dysfunction. *Nature Reviews Neuroscience, 7*(12), 942-951.

Jordan, E. M., & Thomas, D. G. (2017). Contagious positive affective responses to laughter in infancy. *Archives of Psychology*, 1(2): 1-21.

Justin, F. (1932). A genetic study of laughter provoking stimuli. *Child Development*, 3(2), 114-136.

Kaminski, J., Hynds, J., Morris, P., & Waller, B. M. (2017). Human attention affects facial expressions in domestic dogs. Scientific reports, 7(1), 12914. doi:10.1038/s41598-017-12781-x

Karpatschof, B. (2013). Play, but not simply play: The anthropology of play. In Schousboe I. & Winther-Lindqvist (Eds.), *Children's play and development* (pp 251-265). Dordrecht (The Netherlands): Springer.

Kaufman, A. B., & Rosenthal, R. (2009). Can you believe my eyes? The importance of interobserver reliability statistics in observations of animal behaviour. *Animal Behaviour, 78*, 1487-1491. doi:10.1016/j.anbehav.2009.09.014

Keltner, D., & Haidt, J. (1999). Social functions of emotions at four levels of analysis. *Cognition and Emotion*, *13*, 505-521.

Likowski, K. U., Mühlberger, A., Gerdes, A. B. M., Wieser, M. J., Pauli, P., & Weyers, P. (2012). Facial mimicry and the mirror neuron system: simultaneous acquisition of facial electromyography and functional magnetic resonance imaging. *Frontiers in Human Neuroscience*, *6*, 214. http://doi.org/10.3389/fnhum.2012.00214

Livingstone, S. R., Vezer, E., McGarry, L. M., Lang, A. E., & Russo, F. A. (2016). Deficits in the Mimicry of Facial Expressions in Parkinson's Disease. *Frontiers in psychology*, 7:780. doi: 10.3389/fpsyg.2016.00780

Llamazares-Martín, C., Scopa, C., Guillén-Salazar, F., & Palagi, E. (2017). Relaxed open mouth reciprocity favours playful contacts in south american sea lions (*Otaria flavescens*). *Behavioural Processes*, *140*: 87-95. doi: 10.1016/j.beproc.2017.04.007.

MacDonald, S. E. (1994). Gorillas' (*Gorilla gorilla gorilla*) spatial memory in a foraging task. *Journal of Comparative Psychology, 108*, 107-113.

Mancini, G., Ferrari, P. F., & Palagi, E. (2013a). Rapid facial mimicry in Geladas. *Scientific Reports, 3*, 1527. doi:10.1038/srep01527

Mancini, G., Ferrari, P. F., & Palagi, E. (2013b). In play we trust. Rapid facial mimicry predicts the duration of playful interactions in geladas. *PLoS ONE, 8*, e66481. doi:10.1371/journal.pone.0066481

Martin, P., & Caro, T. M. (1985). On the functions of play and its role in behavioral development. *Advances in the Study of Behavior, 15*, 59-103.

Mehu, M., Grammer, K., & Dunbar, R. I. (2007). Smiles when sharing. *Evolution and Human Behavior, 28*, 415-422. doi:10.1016/j.evolhumbehav.2007.05.010

Mundry, R., & Fischer, J. (1998). Use of statistical programs for nonparametric tests of small samples often lead to incorrect P values: examples from animal behaviour. *Animal Behaviour, 56*, 256–259.

Nelson, N. L., & Russell, J. A. (2013). Universality revisited. *Emotion Review, 5*(1), 8-15.

Norscia, I., & Palagi, E. (2011). When play is a family business: adult play, hierarchy, and possible stress reduction in common marmosets. *Primates, 52*(2), 101-104.

Norscia, I., & Palagi, P. (2016). *The missing lemur link: An ancestral step in the evolution of human behaviour*. Cambridge (UK): Cambridge University Press.

Oberman, L. M., Winkielman, P., & Ramachandran, V. S. (2009). Slow echo: facial EMG evidence for the delay of spontaneous, but not voluntary, emotional mimicry in children with autism spectrum disorders. *Developmental science*, 12(4), 510-520.

Palagi, E. (2006). Social play in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): implications for natural social system and interindividual relationships. *American Journal of Physical Anthropology, 129*,418-426. doi:10.1002/ajpa.20289

Palagi, E. (2008). Sharing the motivation to play: the use of signals in adult bonobos. *Animal Behaviour, 75*, 887-896. doi:10.1016/j.anbehav.2007.07.016

Palagi, E., & Cordoni, G. (2012). The right time to happen: play developmental divergence in the two *Pan* species. *PlosONE, 7(12),* e52767. doi:10.1371/journal.pone.0052767

Palagi, E., & Mancini, G. (2011). Play and primates: social, communicative, and cognitive aspects of one of the most puzzling behaviour. *Atti della Società Toscana di Scienze Naturali Serie B, 118*, 121-128.

Palagi, E., & Scopa, C. (2017). Integrating Tinbergen's inquiries: Mimicry and play in humans and other social mammals. *Learning & behavior*, 45(4), 378-389.

Palagi, E., Antonacci, D., & Cordoni, G. (2007). Fine-tuning of social play in juvenile Lowland gorillas (*Gorilla gorilla gorilla*). *Developmental Psychobiology, 49,* 433-445. doi: 10.1002/dev.20219

Palagi, E., Burghardt, G. M., Smuts, B., Cordoni, G., Dall'Olio, S., Fouts, H. N., Reháková-Petru, M., Siviy, S. M., & Pellis, S. M. (2016). Rough-and-tumble play as a window on animal communication. *Biological reviews of the Cambridge Philosophical Society, 91(2),* 311-327. doi: 10.1111/brv.12172

Palagi, E., Nicotra, V., & Cordoni, G. (2015). Rapid mimicry and emotional contagion in domestic dogs. *Royal Society open science, 2,* 150505. doi:10.1098/rsos.150505

Palagi, E., Norscia, I., & Spada, G. (2014). Relaxed open mouth as a playful signal in wild ring-tailed lemurs. *American Journal of Primatology, 76*(11), 1074-1083.

Panksepp, J. (2004). *Affective neuroscience: The foundations of human and animal emotions.* New York: Oxford University Press.

Paquette, D. (1994). Fighting and playfighting in captive adolescent chimpanzees. *Aggressive Behavior, 20*(1), 49-65.

Parkinson, B. (2011). Interpersonal emotion transfer: contagion and social appraisal. *Social & Personality Psychology Compass, 5*, 428-439. doi:10.1111/j.1751-9004.2011.00365.x

Parnell, R. J. (2002). Group size and structure in western lowland gorillas (Gorilla gorilla gorilla) at Mbeli Bai, Republic of Congo. *American Journal of Primatology*, *56*(4), 193-206.

Parr, L. A., & Waller, B. M. (2006). Understanding chimpanzee facial expression: insights into the evolution of communication. *Social Cognitive and Affective Neuroscience*, 1(3), 221-228.

Parr, L. A., Waller, B. M., & Fugate, J. (2005). Emotional communication in primates: implications for neurobiology. *Current Opinion in Neurobiology, 15*, 716-720.

Pellegrini, A. D. (2009). *The role of play in human development*. New York: Oxford University Press.

Pellegrini, A. D., Dupuis, D., & Smith, P. K. (2007). Play in evolution and development. *Developmental review*, *27*(2), 261-276.

Pellis, S. M. (1988). Agonistic versus amicable targets of attack and defense: Consequences for the origin, function, and descriptive classification of play fighting. *Aggressive Behavior, 14*, 85-104. doi:10.1002/1098-2337(1988)14:2<85::AID-AB2480140203>3.0.CO;2-5

Pellis, S. M., & Pellis, V. C. (2009). *The playful brain: venturing to the limits of neuroscience*. Oxford: Oneworld Publications.

Pellis, S. M., Pellis, V. C., & Reinhart, C. J. (2010). The evolution of social play. In C. Worthman, P. Plotsky, D. Schechter & C. Cummings (Eds.), *Formative Experiences: The Interaction of Caregiving, Culture, and Developmental Psychobiology* (pp. 404-431). Cambridge University Press; Cambridge, UK.

Pellis, S. M., & Pellis, V. C. (1996). On knowing it's only play: the role of play signals in play fighting. *Aggressive Violent Behavior, 1*, 249-268. doi:10.1016/1359-1789(95)00016-X

Pellis, S. M., & Pellis, V. C. (1998). The structure-function interface in the analysis of play fighting. In M. Bekoff & J. A. Byers (Eds.), *Play Behavior: Comparative, Evolutionary, and Ecological Aspects* (pp. 115-140). Cambridge University Press, Cambridge, U. K.

Pellis, S. M., & Pellis, V. C. (2016). Play fighting in Visayan warty pigs (*Sus cebifrons*): Insights on restraint and reciprocity in the maintenance of play. *Behaviour*, *153*, 727-747.

Pellis, S. M., & Pellis, V. C. (2017). What is play fighting and what is it good for? *Learning & Behavior*. doi: 10.3758/s13420-017-0264-3

Pellis, S. M., Pellis, V. C., Reinhart, C. J., & Thierry, B. (2011). The use of the bared-teeth display during play fighting in Tonkean macaques (*Macaca tonkeana*): Sometimes it is all about oneself. *Journal of Comparative Psychology*, *125*(4), 393.

Petrů, M., Špinka, M., Charvátová, V., & Lhota, S. (2009). Revisiting play elements and selfhandicapping in play: a comparative ethogram of five old world monkey species. *Journal of Comparative Psychology*, *123*, 250-263. doi:10.1037/a0016217

Power, T. G. (2000). *Play and Exploration in Children and Animals*. Mahwah (New Jersey, US): Lawrence Erlbaum Associates.

Preuschoft, S. (1992). "Laughter" and "smile" in Barbary macaques, *Macaca sylvanus*. *Ethology*, *91*, 220–236.

Preuschoft, S., & Van Hooff, J. A. R. A. M. (1995). Homologizing primate facial displays: A critical review of methods. *Folia Primatologica*, *65*, 121–137.

Preuschoft, S., & van Hooff, J. A. R. A. M. (1997). The social function of "smile" and "laugther": variations across primate species and societies. In U. Segerstrale & P. Molnàr (Eds.), *Nonverbal communication: Where nature meets culture* (pp. 171–189). Mahwah, NJ: Erlbaum.

Reed, L. I., & DeScioli, P. (2017). The communicative function of sad facial expressions. Evolutionary Psychology, 15(1), 1474704917700418.

Reed, L. I., DeScioli, P., & Pinker, S. A. (2014). The commitment function of angry facial expressions. Psychological Science, 25(8), 1511-1517.

Rychlowska, M., Jack, R. E., Garrod, O. G., Schyns, P. G., Martin, J. D., & Niedenthal, P. M. (2017). Functional smiles: Tools for love, sympathy, and war. *Psychological science*, *28*(9), 1259-1270.

Rychlowska, M., Miyamoto, Y., Matsumoto, D., Hess, U., Gilboa-Schechtman, E., Kamble, S., … Niedenthal, P. M. (2015). Heterogeneity of long-history migration explains cultural differences in reports of emotional expressivity and the functions of smiles. *Proceedings of the National Academy of Sciences of the United States of America, 112*(19), E2429–E2436. http://doi.org/10.1073/pnas.1413661112

Sarra, S., & Otta, E. (2001). Different types of smiles and laughter in preschool children. *Psychological reports, 89*(3), 547-558.

Scally, A., Dutheil, J. Y., Hillier, L. W., Jordan, G. E., Goodhead, I., Herrero, J., ... & McCarthy, S. (2012). Insights into hominid evolution from the gorilla genome sequence. *Nature, 483*(7388), 169.

Schmidt, K. L, & Cohn, J. F. (2001). Human facial expressions as adaptations: evolutionary questions in facial expression research. *Yearbook of Physical Anthropology, 44,* 3-24. doi:10.1002/ajpa.2001

Scopa, C., & Palagi, E. (2016). Mimic me while playing! Social tolerance and rapid facial mimicry in macaques (*Macaca tonkeana* and *Macaca fuscata*). *Journal of Comparative Psychology, 130(2),* 153-161. doi:10.1037/com0000028

Siegel, S., & Castellan, N. J. (1988). *Nonparametric statistics for the behavioral sciences* (2nd ed.). New York: McGraw-Hill.

Sonnby-Borgström, M. (2016). Emotional mimicry: Underlying mechanisms and individual differences. In U. Hess & A. Fischer (Eds.), *Emotional mimicry in social context* (pp 125-161). Cambridge (UK): Cambridge University Press.

Spinka, M., Newberry, R. C., & Bekoff, M. (2001). Mammalian play: training for the unexpected. *Quarterly Review of Biology,76,* 141-167. doi:10.1086/393866

Stanton, M. A., Lonsdorf, E. V., Pusey, A. E., Goodall, J., & Murray, C. M. (2014). Maternal behavior by birth order in wild chimpanzees (*Pan troglodytes*) increased investment by first-time mothers. *Current Anthropology, 55*(4), 483-489.

Stokes, E. J., Parnell, R. J., & Olejniczak, C. (2003). Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). *Behavioral Ecology and Sociobiology, 54(4),* 329-339. doi: 10.1007/s00265-003-0630-3.

Strack, F., Martin, L. L., & Stepper, S. (1988). Inhibiting and facilitating conditions of the human smile: a non-obtrusive test of the facial feedback hypothesis. *Journal of Personality and Social Psychology*, *54*(5), 768.

Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's Information Criterion. *Behavioral Ecology and Sociobiology*, *65,* 13-21. doi:10.1007/s00265-010-1037-6

Tsao, D.Y., Moeller, S., & Freiwald, W.A. (2008). Comparing face patch systems in macaques and humans. *Proceedings of the National Academy of Sciences, 105,* 9514-19519.

van Hooff, J. A. R. A. M., & Preuschoft, S. (2003). Laughter and smiling: the intertwining of nature and culture. In F. B. M. de Waal & P. L. Tyack (Eds.), *Animal Social Complexity* (pp. 260-287). Cambridge Massachusetts: Harvard University Press.

van Lawick-Goodall, J. (1968). The behavior of free living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs 1*, 161–311.

Wagenmakers, E. J., Beek, T., Dijkhoff, L., Gronau, Q. F., Acosta, A., Adams Jr, R. B.… & Zwaan. R. A. (2016). Registered Replication Report: Strack, Martin, & Stepper (1988). *Perspectives on Psychological Science, 11*(6), 917-928.

Waller, B. M., & Cherry, L. (2012). Facilitating play through communication: significance of teeth exposure in the gorilla play face. *American Journal of Primatology, 74,* 157-164. doi:10.1002/ajp.21018.

Waller, B., & Dunbar, R. I. M. (2005). Differential behavioural effects of silent bared teeth display and relaxed open mouth display in chimpanzees (*Pan troglodytes*). *Ethology, 111*, 129-142. doi:10.1111/j.1439-0310.2004.01045.x

Watts, D. P., Pusey, A. E. (1993). Behavior of juvenile and adolescent great apes. In M. E. Pereira, & L. A., Fairbanks (Eds.), *Juvenile Primates - Life History, Development, and Behavior* (pp. 148-167). New York: Oxford University Press.

Weisfeld, G. E. (1993). The adaptive value of humor and laughter. *Ethology and Sociobiology, 14*(2), 141-169.

Whiten, A., McGuigan, N., Marshall-Pescini, S., & Hopper, L. M. (2009). Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philosophical Transactions of the Royal Society of London B*: *Biological Sciences, 364*, 2417–2428. doi:10. 1098/rstb.2009.0069

Wieser, M. J., & Brosch, T. (2012). Faces in Context: A Review and Systematization of Contextual Influences on Affective Face Processing. *Frontiers in Psychology, 3,* 471. http://doi.org/10.3389/fpsyg.2012.00471

Yamagiwa, J., Kahekwa, J., & Basabose, A. K. (2003). Intra-specific variation in social organization of gorillas: implications for their social evolution. *Primates, 44,* 359-69. doi:10.1007/s10329-003-0049-5

Figure legends

Figure 1 - Scheme illustrating the criteria used to evaluate the attentional state of the observer in relation to the perception of facial expressions. When the observer was in front of the trigger (direct visual contact condition) we considered the stimulus as perceived. When the observer was not in direct visual contact condition respect to the trigger we considered the stimulus as not perceived. All the cases of lateral views were discarded from the analyses.

Figure 2 - Mean values (±SE) of the Full Play Face Index (FPF-PF/FPF+PF) calculated for chimpanzees and gorillas. PF=Play Face; FPF=Full Play Face

Figure 3 - Mean duration (±SE) of both Play Face and Full Play Face in chimpanzees and gorillas.

Figure 4 - Mean frequency (±SE) of Play Face and Full Play Face in chimpanzees (a) and gorillas (b) performed by the observer within 1 sec and between 1-5 secs after the occurrence of the stimulus both when the observer was in direct visual contact with the trigger (Rapid Facial Mimicry, RFM; Delayed Facial Mimicry, DFM) and when he/she did not visually perceive the stimulus by the trigger.

Figure 5 - Mean number (±SE) of congruent (PF→PF, FPF→FPF) and incongruent (PF→FPF, FPF→PF) responses during RFM in chimpanzees and gorillas. PF=Play Face; FPF=Full Play Face

Figure 6 - Mean duration (±SE) of play session in chimpanzees (a) and gorillas (b) in i) play signals not visually perceived by the observer, ii) presence of at least one signal perceived by the observer but not followed by an event of RFM, and iii) presence of at least one event of RFM. RFM=Rapid Facial Mimicry

Supplementary Video RFM chimpanzees. The video shows two subjects playing. A play face (PF) is performed by the individual on the right and is followed by a PF rapid response (RFM) of the individuals on the left.

Supplementary Video RFM gorillas. The video shows two subjects playing. A full play face (FPF) is performed by the individual on the left and is followed by a FPF rapid response (RFM) of the individuals on the right.